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GROWTH, BEHAVIOUR OF BROODS AND WEATHER-RELATED VARIATION IN BREEDING PRODUCTIVITY OF CURLEW SANDPIPERS *CALIDRIS FERRUGINEA*

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Growth and survival of chicks and movements of broods were studied in Curlew Sandpipers in N.E. Taimyr, Siberia, in 1991. Breeding was synchronised, 73% of 30 clutches hatching during 10-15 July. Nests were distributed clumped in dry frost-heaved tundra. Broods were tended by females only and moved from the nest sites to low-lying wet areas up to 2.4 km away during the first week of life. Here, they often formed aggregations of 2-6 broods with females cooperating in predator defence. In 1991 (a lemming peak year), both clutch and chick survival were high, and breeding productivity was c. 2 fledglings per female. Chicks fledged in 14-16 days, and body mass growth was best described by a logistic curve. The growth rate constant K_L was 0.314, which is high compared to similar-sized waders studied elsewhere. Growth rate was reduced during cold weather, as was the availability of surface-active arthropods which form the main food source for chicks. Effects of weather on chick survival and breeding productivity were examined by correlating data on annual variation in the proportion of juveniles among wintering birds in South Africa with 18 years of summer weather records from the core of the Taimyr breeding area. After allowing for an effect of three-yearly cyclic variation in lemming abundance on predation of eggs and young by arctic foxes and skuas, breeding productivity was positively correlated with mean temperature in Taimyr during 11-20 July, the period when most young chicks are present in the tundra. Weather thus seems to have effects on chick survival both widespread and large enough to be detected in the wintering areas, and the combination of (inferred) predation pressure and weather conditions during the fledging period explains a large part of the variation in breeding productivity found in this species. We found no correlations between productivity and weather during the pre-laying period, in contrast to several studies on arctic-breeding geese.

Key words: *Calidris ferruginea* - Siberia - Taimyr - growth - chicks - brood aggregations - brood movements - weather - breeding productivity

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INTRODUCTION

The Curlew Sandpiper *Calidris ferruginea* is a breeding bird of arctic tundras in northern Siberia, between the Yamal Peninsula in the west and the Chukchi Peninsula in the east. Aspects of its breeding biology have been described by Portenko (1959), Holmes & Pitelka (1964), Tomkovich (1988), and Tomkovich *et al.* (1994), but growth and survival of chicks and behaviour of family parties have not been intensively studied. The species is a long-distance migrant wintering in (sub)tropical and south-temperate latitudes from Africa to New Zealand (Hayman *et al.* 1986). It has been noted for the highly fluctuating numbers of juvenile birds occurring on autumn migration in western Europe (Stanley & Minton 1972; Roselaar 1979) and in winter in southern Africa (Summers & Underhill 1987). These fluctuations show a three-year periodicity which is synchronous with fluctuations in juvenile output in other wader species and Brent Geese *Branta bernicla* breeding on the Taimyr Peninsula (Underhill *et al.* 1989). The 'prey-switching hypothesis' (Roselaar 1979; Summers 1986; Dhondt 1987) explains this pattern as a switch made by predators from a diet of lemmings to birds' eggs and young after a decrease in lemming abundance. During a three-year lemming cycle, breeding success is poor in the year after a lemming peak, when lemming numbers have decreased sharply and predators are abundant following good reproduction. In the next two years predation on birds is much lower, due to an increase of lemmings combined with low numbers of predators in the second, and an abundance of lemmings in the third year. The hypothesis has received support with respect to waders from a comparative field study in Taimyr during a lemming peak and a lemming low year (Underhill *et al.* 1993).

However, breeding success is not guaranteed when predation is low (Dhondt 1987). In arctic-breeding geese, energy stores upon arrival or feeding conditions during the pre-laying period may affect clutch size (Ebbinge 1989, 1990; Ganter & Cooke 1996). For waders, in which clutch size is less variable than in geese, weather during the fledging period may be an important factor, by influencing survival of the chicks. In this paper, we describe growth and development of chicks and reproductive success of Curlew Sandpipers in a study area on the Taimyr Peninsula in 1991, a lemming peak year (Underhill *et al.* 1993). In this year, we found a correlation between growth rate of chicks and local weather conditions. Since growth rates may be reflected in chick survival, we extended the scope of the study by analysing data on Curlew Sandpiper breeding productivity, recorded in a non-breeding area over 18 years, for

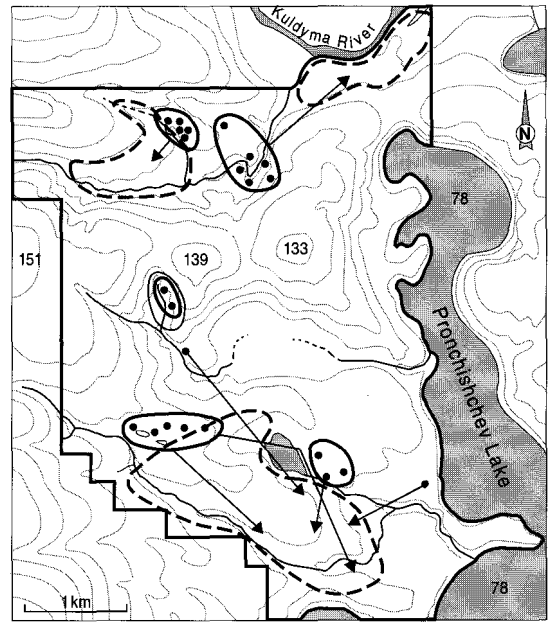

Fig. 1. The study area west of the northern extension of Pronchishchev Lake, with locations of Curlew Sandpiper nests (dots). The thick unbroken line delineates the area covered during searches for broods later in the season (15.6 km^2); the northernmost and southernmost 0.8 km^2 were not searched for nests. Broods from clusters of nests within the solid circles joined into loose aggregations and were found within the areas bounded by broken lines during most of the fledging period. Arrows denote general direction of movement from nesting to brood-rearing areas. Heights (in m a.s.l.) of the lake and the two highest points in the study area, as well as 10 m altitude contours (stippled), are given.

correlations with weather conditions during the main chick-rearing period.

STUDY AREA

Curlew Sandpipers were studied between 15 June and 8 August 1991, near Pronchishchev Lake in the northeastern part of the Taimyr Peninsula (75°16'N, 112°28'E), 30 km from the Laptev Sea. The area consisted of moderately dry hilly arctic tundra (Chernov 1985), drained by three small streams (Fig. 1). Watersheds and upper parts of slopes were generally well-drained and consisted of sparsely vegetated frost-heaved and frost-boiled tundra. Wetter areas occurred on the lower parts of slopes and in marshes in valleys and on level parts of watersheds (see Schekkerman & Van Roomen 1995 for a detailed description). Snow cover dropped below 90% on 21 June, and reached 50% on 27 June and 5% on 3 July (Underhill *et al.* 1993). 1991 was a lemming peak year in the study area, with lemming densities of up to 400 animals ha^{-1}. Snowy Owls *Nyctea scandiaca*, Pomarine Skuas *Stercorarius pomarinus*, Long-tailed Skuas *S. longicaudus,* and Arctic Foxes *Alopex lagopus* fed almost exclusively on the abundant lemmings and reproduced well (Underhill *et al.* 1993).

METHODS

Field procedures

Curlew Sandpiper nests were located in a 14 km^2 area by watching females return after disturbance. Nests were marked, and clutch size and egg measurements were recorded. Eggs were marked and weighed at intervals to determine the rate of mass loss during incubation and the date of clutch completion (Underhill *et al.* 1993). Incubating females were trapped with a small clap-net. They were weighed and measured, and given a combination of metal and colour-rings for individual recognition. Most were also dyed with picric acid on the left underwing.

Survival of clutches was monitored by visits to nests at approximately three day intervals. Towards hatching, nests were visited more frequently to establish their outcome and ring the chicks. After hatching, a slightly extended (15.6 km^2; Fig. 1) area was regularly searched for females with broods. Chicks were (re)captured whenever possible, and body mass (spring balance), wing length (maximum chord, after the primary tips had appeared), length of bill (exposed culmen) and tarsus were measured.

The presence of chicks was fairly easily ascertained from the alarm behaviour of the females. Locations of broods were recorded relative to a 250 x 250 m grid with the aid of a 1:25 000 map. Minimum brood size was determined by observation from a distance or from captures, though often the number of chicks alive could not be assessed with certainty. When repeatedly fewer chicks were observed in a brood than expected from the number of eggs hatched, it was assumed that the missing chicks had died. In this way, chicks were classified as 'alive', 'fate unknown', or 'dead' at five-day age intervals.

Maximum and minimum air temperatures were recorded daily at the camp, using a thermometer placed 1 cm above the ground and shaded from the sun. The abundance and activity of surface-dwelling tundra arthropods was monitored using 10 pitfall traps, placed along a 100 m transect in moderately dry tundra. They were emptied every day around midnight in June and on average every three days in July, and the animals were classified into broad taxonomical groups and counted (Underhill *et al.* 1993).

Growth

Logistic growth curves were fitted to data from chicks of which the age was known to within 24 h. Because of lack of independence between data points obtained from individual chicks, approximate standard errors for the parameter estimates were derived using the jackknife technique, by serial exclusion of individual chicks from the dataset (Sokal & Rohlf 1981). The growth curves (mainly those for bill and wing length) were used

to estimate the hatching date for broods that were found only after hatching.

To analyse the relationship between growth and weather conditions, growth rates were calculated for chicks captured and measured twice within a period of at least two and at most seven days. To take account of the sigmoid shape of the growth curve and make growth rates comparable for different ages, they were converted to a 'growth index' by dividing the observed growth by the growth expected on the basis of the average logistic curve for all individuals (equation 19 in Schoener & Schoener 1978). The indices were then regressed on the average temperature during the interval between captures. Because chicks from the same brood do not produce independent observations, hierarchical linear modelling was applied (Byrk & Raudenbusch 1992), which takes into account that chicks and broods represent different error levels in the data. The program MLN (Institute of Education 1995) was used for model fitting.

Long-term weather and productivity data

Data of Curlew Sandpiper breeding productivity, measured as the percentage of first-year birds in samples trapped for ringing on wintering grounds in South Africa, were taken from Summers & Underhill (1987), Underhill (1990), and Underhill & Oatley (1995). To investigate relationships between breeding productivity and weather conditions on the breeding grounds, data for 1977-1990 were available from a weather station near the delta of the Pyasina River in NW Taimyr (73°34'N, 86°15'E). These comprised daily minimum and maximum temperature (averaged to daily mean temperature), daily mean wind speed (based on four measurements per day), and daily precipitation in June, July and August of each year. In addition, the date at which snow depth decreased to 50% of the value on 1 June was used as an estimate of the timing of snow melt. After 1990, data recording at the weather station was discontinued, but additional temperature measurements for 1990-1994 were available from Lydia Bay, 50 km to the NE (B.S. Ebbinge & B. Spaans unpubl.). In June-July 1990, daily mean temperatures here and at the weather station showed a tight correlation ($r_{48} = 0.92$, $P < 0.001$), and a linear regression equation was used to convert Lydia Bay temperatures to weather station values for 1991-1994. Wind speed data were not available for these years.

Relations between summer weather and the proportion of first-year birds in the winter population were explored using logistic regression. Levels of 'inferred predation pressure' (IPP) were based on qualitative descriptions of lemming abundance on the Taimyr Peninsula (Summers & Underhill 1987; Ryabitsev 1993; Yurlov 1993; Tomkovich 1994ab, 1995). They show a pronounced periodicity with low IPP during a lemming peak every third year, followed by a decline in lemming abundance leading to high IPP. We assumed that predation exerts its greatest effect on productivity in the egg stage, while weather is more likely to affect the survival of chicks, and incorporated IPP into the regression models before assessing the effects of weather. Both linear and quadratic effects of weather variables (mean temperature and mean wind speed during 10-day periods) were considered, as well as their interactions with IPP, using a forward selection procedure. Analyses were carried out with Genstat 5.3 (Genstat 5 Committee 1993).

RESULTS

Breeding density, phenology and breeding success in 1991

Curlew Sandpipers were already present at Pronchishchev Lake upon our arrival on 15 June. Twenty-five nests were found in the study area in 1991, as well as 10 additional broods of which 6-8 were assumed to have hatched within its boundaries. With a density of c. 2.3 breeding females per km^2, the Curlew Sandpiper was the most abundant wader species in the area (Underhill *et al.* 1993). Twenty-four (77%) of 31 clutches were completed between 19 and 27 June, and the remainder between 3 and 8 July (median date 25

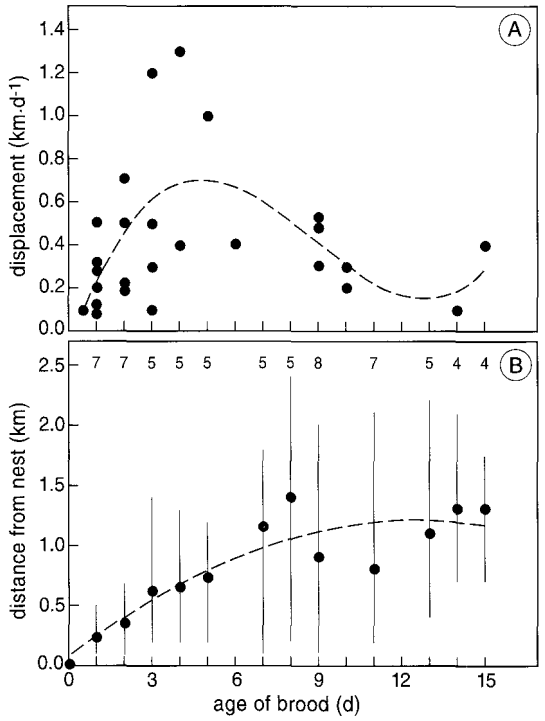

Fig. 2. Displacements of Curlew Sandpiper broods in relation to age. A: Straight-line distances between locations observed on consecutive days. B: Mean and range of distances between brood locations and nest site (sample sizes given on top). Broken lines show polynomial curves fitted to lead the eye, using hierarchical linear modelling (taking into account that broods provided multiple data points); both quadratic (B) and cubic (A) terms were significant at $P < 0.05$.

June). Hatching took place between 10 and 26 July, with 73% of 30 clutches hatching between 10 and 15 July, and with the peak and median on 12 July. Twenty-two clutches contained four eggs, and one each contained three, two and one egg (mean clutch size 3.76, SD 0.72, n = 25).

Curlew Sandpiper chicks fledged at an average age of 15 days. Out of six broods checked at 13 days of age, none were able to fly ≥20 m; these figures were 1/3, 2/3 and 5/5 for broods of 14, 15 and 16 days, respectively. Females incubated and tended broods alone. Males were last observed singing on 2 July, and none were seen in the study area after 10 July. Females stayed with the brood until shortly after fledging; they were seen accompanying fledged chicks of 16 (5x), 17 (2x) and 20 days of age. Small numbers of westward-migrating females (either failed breeders or successful birds migrating ahead of their young) were seen between 20 July and 5 August, and small flocks of migrant juveniles from 27 July onwards until our departure on 8 August.

Table 1. Percentage of Curlew Sandpiper broods observed in brood aggregations according to age of the chicks.

age (d)	n	% in aggregation
0-3	22	5%
4-6	16	50%
7-9	17	88%
10-12	11	73%
13-15	12	92%

Nest success was high, none of 25 clutches being lost to predation or desertion during 235 nest-days. More than 90% of the eggs hatched; part of the few losses were due to eggs being damaged during handling. The fate of a large proportion of the chicks was not known, but chick mortality seemed to be highest during the first five days after hatching (Schekkerman & Van Roomen 1995). Of 23 Curlew Sandpiper broods hatched before 25 July, 10 (43%) produced at least one fledged juvenile (total number fledged between 18 and 74). If it is assumed that all chicks alive at day 10 survived to fledging, at least 16 broods (70%) were succesful and 28-79 chicks fledged, 1.2-3.4 per breeding female. Since some broods may have moved beyond the limits of the study area, brood survival may have been underestimated and productivity was probably around two chicks per breeding female.

Habitat choice and brood movements

Nests were situated in moderately dry frost-heaved tundra, usually in the vicinity of a patch of wetter tundra with growth of sedges, where the females did most of their foraging. Nest sites

were highly aggregated (Fig. 1), much more so than the distribution of dry tundra would suggest, and corresponding to the distribution of snow-free patches early in the season. Broods left the nest within a day after hatching. In general, they moved away from the nesting sites to lower-lying moist areas where they remained during the latter part of the fledging period (Fig. 1). Distances between brood locations on consecutive days were small during the first few days, but increased rapidly to a maximum at three to five days of age (Fig. 2a). Thereafter, movements became less directional, resulting in smaller daily displacements. Distances between the locations of broods and their nest site did not increase further after the first week (Fig. 2b). The maximum observed distance from the nest was 2.4 km, but some broods may have left the study area and moved beyond our attention.

The areas used by broods during the latter half of the fledging period were generally open, with little microrelief, allowing free views of the surroundings. They were located mainly on the lower, less steep slopes of hills and in wide valleys. In contrast to the nesting habitat, these sites were rather wet, with sedges dominating the vegetation.

In the brood-rearing areas, broods tended to join into loose aggregations with other families of Curlew Sandpipers and, less often, other species. Out of 78 observations of broods, 43 (65%) were in aggregations, which usually consisted of 2-4 (maximum 6) families. Distances between broods in aggregations varied between approximately 10 and 200 m, but were rarely so small that chicks intermingled. The females collaborated when alarming for, and mobbing, skuas and human observers, although each returned to her own chicks when predators were not in the vicinity. No exchange of ringed chicks between broods was observed. The composition of aggregations was rather stable, but changes in the number and identity of participants did occur. Although they often involved females which had bred close together, they were not formed directly after hatching, but mainly between four and seven days later, coinciding with the arrival in the brood-rearing areas (Table 1). Several aggregations included one or two broods of Turnstone *Arenaria interpres* (5x), Little Stint *Calidris minuta* (4x), or Sanderling *C. alba* (1x).

Growth and weather conditions

Body mass showed little change during the first day after hatching (Fig. 3). Therefore, chick masses determined in the first 24 h after hatching were not used in fitting the mass growth curve. Bill length and tarsus length increased from the first day onwards, and all data were used. Logistic curves produced a slightly better description of the slow initial increase in body mass and bill length and a more realistic estimate of the asymptotes than Gompertz' curves. At fledging, the young had reached 95% of the mean mass of adults wintering in Africa, while bill and wing length continue to increase considerably after fledging (Table 2). As growth may be similar among chicks within the same broods, the jacknifed standard errors presented in Table 2 could be underestimations. However, jacknifing standard errors by serially excluding whole broods from the dataset instead of individual chicks produced similar results (e.g. for body mass: $A = 50.3 \pm 1.2$, $K = 0.33 \pm 0.03$, $T = 5.58 \pm 0.27$).

Daily mean air temperature reached maximum values (12-20°C) between 10 and 19 July. There was a distinct cold spell from 20 to 25 July, with mean temperatures of 2-5°C, strong winds, and rain and snowfall on several days. Ambient temperature affected growth rates of both body mass and bill length in young Curlew Sandpipers (Fig. 4). Although largely dependent on one datapoint, the relationship seemed curvilinear, with slower growth and even mass loss at the lowest temperature (regression equations derived by hierarchical linear modelling: mass, $y = -1.577 + 0.4053x - 0.01544x^2$, $SE_{B1} = 0.1058$, $t_9 = 3.83$, $P < 0.01$, $SE_{B2} = 0.00482$, $t_9 = 3.20$, $P < 0.02$; bill, $y = -0.5896 + 0.2659x - 0.00976x^2$, $SE_{B1} = 0.0667$, $t_6 = 3.98$, $P < 0.01$, $SE_{B2} = 0.0031$, $t_6 = 3.16$, $P < 0.02$). As the tarsus is almost fully grown in chicks of a week old, and very few pairs of meas-

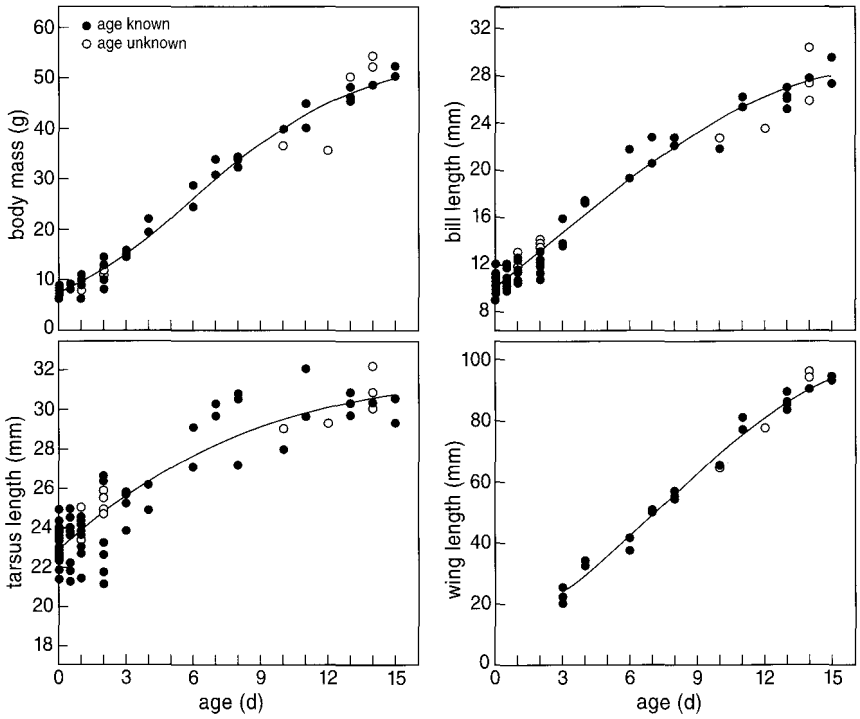

Fig. 3. Growth of body mass, bill length, tarsus length, and wing length in Curlew Sandpiper chicks. Black dots represent chicks of known age, and only these were used in fitting the growth curves. Open dots represent chicks of unknown hatch date that were captured twice, and in which the age at first capture was estimated by comparing their measurements to those of known-age chicks. Growth curve parameters are given in Table 2.

Table 2. Growth parameters for chicks of Curlew Sandpiper. The number of chicks contributing data (n), the three parameters of the logistic growth equation ($y(t) = A/[1 + e^{-K(t - T)}]$) and their standard errors, and the size at hatching (Y_h), at fledging (Y_f), and when adult (Ad; Wymenga *et al.* 1990), are given.

variable	n	A	SE_A	K	SE_K	T	SE_T	Y_h	Y_f	Ad
body mass	29	52.09	1.54	0.314	0.020	5.89	0.32	8.2	49.6	52
bill length	50	30.12	1.25	0.205	0.018	3.15	0.53	10.8	27.8	38
tarsus	50	31.82	0.76	0.157	0.030	-6.02	0.80	23.2	30.8	31
wing	20	107.8	4.0	0.260	0.021	7.59	0.39	17.0	94.5	132

urements for wing length were available, no attempts were made to relate tarsus and wing growth to temperature.

The daily number of arthropods caught in the pitfall traps was closely related to mean temperature (Fig. 5), both when viewed over the entire summer period (Poisson regression; log (y) = 3.040 + 0.1755x, change in deviance = 1119.7, $P < 0.001$) and in the period when most chicks were present (10-31 July, log (y) = 4.408 + 0.069x; change in deviance = 68.5, $P < 0.001$). On cold days, the availability of food for Curlew Sand-

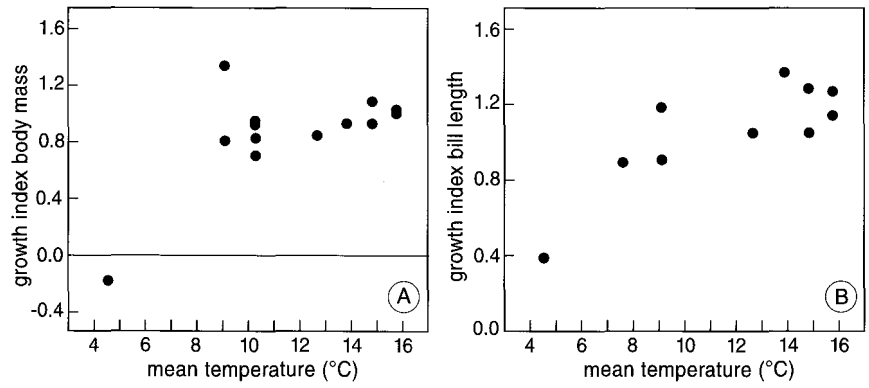

Fig. 4. Growth rate indices (observed / expected growth) for body mass (A) and bill length (B) in relation to average temperature. Statistics in text.

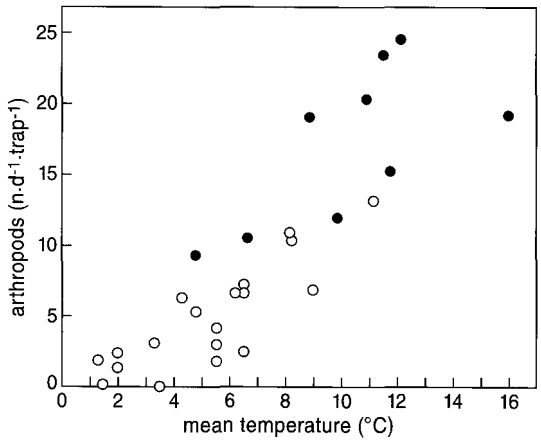

Fig. 5. Relationship between mean daily temperature and the number of arthropods caught in pitfall traps (mites and springtails ≤1.5 mm excluded), 16 June - 6 August 1991. Black dots are data points from the period in which most chicks were present (10-31 July). Statistics in text.

piper chicks, which foraged visually on surface-active prey, was thus markedly reduced.

Annual variation in breeding success

Because chick mortality was highest in the first week, weather effects on breeding productivity are most likely to be found shortly after the main hatching period, when many young chicks are present. In 1991, most Curlew Sandpiper chicks hatched between 10 and 15 July. Hatching dates elsewhere in Taimyr and in other years (Table 3) show a similar phenology, with a tendency towards later dates in northern Taimyr and in years of late snow melt, notably 1992 and 1994. Hence, for the core breeding area which extends between 73°N and 75°N in Taimyr (Rogacheva 1992; Lappo 1996), it can be expected that if weather conditions affect chick survival, the second decade of July will be the critical period. Mean temperature in this period was therefore used as the primary weather variable to test for associations with variation in breeding productivity.

Summers & Underhill (1987) showed that Curlew Sandpiper breeding productivity during 1969-1986, measured in the wintering area, was significantly associated with lemming abundance and inferred predation pressure (IPP). They modelled IPP as a two-state variable, being either low (in years when lemming abundance is either the same or higher than in the previous year) or high (after a fall in lemming abundance). For 1977-1994 (the years for which weather data were available) as well, the effect of IPP proved highly significant (Table 4a). Mean temperature during 11-20 July significantly improved the fit of the logistic regression model containing IPP (Table 4a). There was also a significant interaction between

Table 3. Literature data on hatching phenology of Curlew Sandpipers on the Taimyr Peninsula. Hatching dates were observed directly or estimated from egg-flotation, egg-weights or chick biometrics. Sites are ordered according to latitude.

			hatching date				
site	coordinates		year	*n*	range	median	reference
Medusa Bay	73°04'N	80°30'E	1994	18	8.7 - 17.7	12.7	Günther & Hertzler unpubl.
Medusa Bay	73°04'N	80°30'E	1996	53	6.7 - 20.7	13.7	Tulp *et al.* 1997
Uboinaya River	73°37'N	82°20'E	1984	14	6.7 - 17.7	11.7	Tomkovich 1995
Pyasina Delta	74°08'N	86°45'E	1990	8	7.7 - 20.7	16.7	Hötker 1995
Pyasina Delta	74°08'N	86°45'E	1993	5	5.7 - 13.7	11.7	vDijk & Venema unpubl.
Pyasina Delta	74°08'N	86°45'E	1994	10	17.7 - 2.8	24.7	Vonk & Duiven unpubl.
Pyasina Delta	74°08'N	86°45'E	1995	12	10.7 - 24.7	13.7	Mulder unpubl.
Pronchishchev Lake	75°16'N	112°28'E	1991	30	10.7 - 26.7	12.7	this study
Pronchishchev Lake	75°16'N	112°28'E	1992	20	16.7 - 31.7	21.7	Spiekman & Groen 1993
Sterlegov Cape	75°26'N	89°08'E	1990	3	13.7 - 16.7	15.7	Hötker 1995
Sterlegov Cape	75°26'N	89°08'E	1994	5	16.7 - 4.8	24.7	Tulp *et al.* 1998
Knipovich Bay	76°05'N	98°32'E	1990	24	8.7 - 25.7	19.7	Tomkovich *et al.* 1994
Knipovich Bay	76°05'N	98°32'E	1991	19	30.6 - 30.7	17.7	Tomkovich *et al.* 1994
Knipovich Bay	76°05'N	98°32'E	1992	4	23.7 - 31.7	28.7	Tomkovich *et al.* 1994

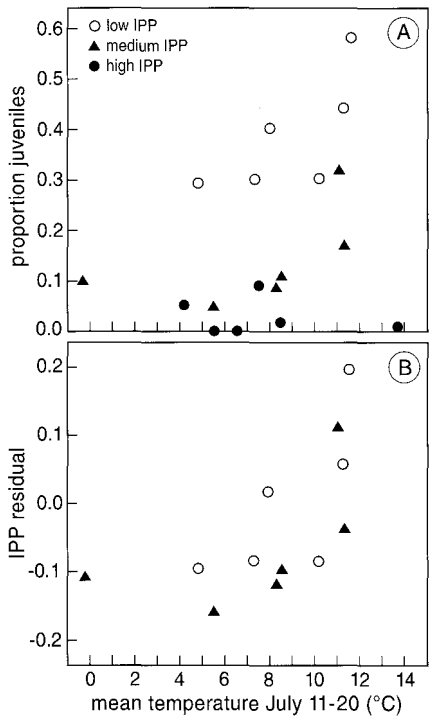

Fig. 6. Relationship between mean temperature at the Pyasina river, Taimyr, between 10-20 July and the proportion of juvenile Curlew Sandpipers in winter catches in South Africa, divided into years with low, medium and high inferred predation pressure (IPP). A: untransformed data, B: residual productivities for years with medium and low IPP, after correcting for IPP effects. Statistics in Table 4b.

IPP and temperature; in years of high IPP, the temperature effect was much weaker than in other years.

However, there are no a priori reasons for assuming predation levels to be the same in intermediate and peak lemming years, and the data suggested higher productivities in lemming peak years than in the preceding years (Fig. 6a). When the category 'low IPP' was split into 'low' (in lemming peak years) and 'medium' (in the preceding years) for 1977-1994, the fit of the logistic regression model was significantly improved (Table 4b), and the mean productivities for the low

Table 4. Logistic regression models for the breeding productivity of Curlew Sandpipers, measured as the proportion of juveniles in ringing samples of birds wintering in South Africa (n = 18 years). Explanatory variables tested were IPP (2 levels in (a), 3 levels in (b), mean temperature between 10 and 20 July and its square, and the interaction terms IPP.temperature and IPP.temperature^2. In model (b), IPP was entered first as a 2-level variable, after which a 3rd level was nested within the original level 2, to show the improvement of the fit associated with this 3rd level. The changes in deviance are additive, reflecting the building-up of the models; the regression coefficients are those for the final model including all significant terms (texts between brackets clarify when IPP terms apply).

	parameter	change in deviance	*df*	*P*	estimates of coefficient	SE
(a)	constant				-2.91	2.17
	IPP (2 levels)	185.20	1	< 0.001	0.56	2.28 (IPP not high)
	temperature	39.62	1	< 0.001	-0.087	0.292
	IPP.temperature	7.60	1	< 0.01	0.241	0.302 (IPP not high)
	residual	133.10	14			
	total	365.52	17			
(b)	constant				-1.74	1.54
	IPP (2 levels)	185.20	1	< 0.001	0.83	1.44 (IPP not high)
	IPP (3rd level)	95.87	1	< 0.001	-1.31	0.304 (IPP medium)
	temperature	22.27	1	< 0.001	-0.395	0.277
	temperature .IPP (2 levels)	6.08	1	< 0.02	0.277	0.187 (IPP not high)
	temperature .IPP (3rd level)	0.01	1	> 0.5		
	temperature^2	11.78	1	< 0.01	0.018	0.012
	residual	44.31	11			
	total	365.52	17			

and medium IPP levels differed significantly from each other (t_{10} = 2.66, P < 0.05).

Adding mean temperature between 10 and 20 July to the regression model containing three levels of IPP again significantly improved its fit (Table 4b). The temperature effect was absent in years of high IPP, while it was of similar magnitude in years of low and medium IPP (interaction temperature 3rd-level IPP n.s.; Table 4b). Furthermore, the relationship between temperature and productivity was curvilinear, because the effect of temperature squared was also significant. Breeding productivity was highest in years when average mid-July temperatures at the Pyasina River rose above 7-10°C (Fig. 6b). IPP alone explained 77% of the total deviance in the data, and adding temperature effects increased this to 88%.

For 14 years (1977-1990) for which mean wind speed during 11-20 July was available, this factor (and its interaction with IPP) increased the model fit even further than did temperature, to an explained deviance of 98%. However, in view of the small number of degrees of freedom left for the residual and the fact that the parameter estimates were biologically unbelievable and sensitive to the exclusion of some years from the data, this model is not presented here.

Mean temperature and wind speed during 11-20 July were not significantly different between years with low, medium or high IPP (ANOVA,

temperature $F_{2,15} = 0.30$, $P = 0.74$; wind speed $F_{2,11} = 0.49$, $P = 0.62$). So, the correlations between breeding productivity and weather were not caused by an association between weather and the phase of the lemming cycle.

The selection of the second decade of July as the period to correlate breeding productivity and weather was made a priori, based on the sandpipers' breeding phenology. We also explored possible associations between productivity and weather in other periods of the birds' presence in the tundra, by calculating the correlation between the residual productivities after correcting for IPP (3 levels) with the date of snow melt and mean temperature, wind speed, and precipitation for each decade of June, July and August. Even without allowing for the fact that this involves multiple simultaneous comparisons, the correlations were not significant ($P \geq 0.16$) for 10-day periods other than the second decade of July.

DISCUSSION

Habitat choice and behaviour of families

The occurrence of brood aggregations in Curlew Sandpipers was earlier described by Haviland (1915) and Soloviev & Tomkovich (1992, in press). Once they had arrived in the same area of preferred habitat, broods tended to stay relatively close together, and females cooperated in predator defence. Because Curlew Sandpiper females care for the eggs and young without help of the male (Portenko 1959; Holmes & Pitelka 1964; Tomkovich 1988) and stay with the brood until fledging, brood aggregations do not allow some of the adults to depart earlier, as was suggested for Bristle-thighed Curlews *Numenius tahitiensis* by Lanctot *et al.* (1995). Curlew Sandpipers may benefit from forming aggregations through shared vigilance and greater effectiveness of cooperative mobbing of predators. Soloviev & Tomkovich (in press) reported that Curlew Sandpipers were the most likely to occur in brood associations among five wader species present in their study area, and that they often joined other species that are more aggressive towards predators. In our study area, Turnstones sometimes served as such an 'umbrella species', but we did not observe associations with the even bolder Grey Plover *Pluvialis squatarola*, perhaps because these hatched c. 10 days later on average.

Movements of broods from nesting sites to rearing areas with a different (often wetter) vegetation type have been described for several arctic waders (Holmes 1966; Parmelee *et al.* 1968; Nettleship 1973; Flint & Kondratiev 1977; Ashkenazie & Safriel 1979; Miller 1983). Brood movements in precocial birds have been explained both as a means of locating good feeding sites (e.g. Erikstad 1985; Galbraith 1988), and to avoid attracting predators by continuous presence at one site. Under the predation hypothesis, daily brood movements should increase with age as the chicks become more valuable to the parent (Sonerud 1985). Contrary to this, brood movements in Curlew Sandpipers were largest in the first week of the chicks' life. In addition, families are more easily visible from a distance in the flat greenish marshes and sedge tundra than in the rugged brownish frost-heaved tundra. This suggests that in Curlew Sandpipers brood movements are not primarily an anti-predation adaptation, and that they are better explained by differences in food availability between nesting sites and chick-rearing areas. Hötker & Nehls (1995) and Tulp *et al.* (1997, 1998) found more arthropods in pitfalls and soil samples in moist grassy tundra and marshes than in dryer vegetations at three sites in NW Taimyr. Similarly at Barrow, Alaska, both adult insects and larvae were more common in July in lowland marshes, which were frequented most by Dunlin *Calidris alpina* broods, than in upland tundra (Holmes 1966).

Growth rate

Growth in Curlew Sandpiper chicks was rapid compared to that in other wader species. Beintema & Visser (1989a) described the allometric relationship between asymptotic mass (A, in g) and the Gompertz' growth coefficient in 15 species: $K_G = 0.390\ A^{-0.312}$. Conversion of the logistic rate

parameter K_L to K_G (Ricklefs 1973) yields K_G = 0.213 for Curlew Sandpipers, 71% higher than the value (0.114) expected on the basis of this relationship. Apart from the fact that the allometric equation includes data on plovers (Charadriidae), which generally grow slower than sandpipers (Scolopacidae), the difference may be related to the high breeding latitude (Beintema & Visser 1989a). The short summer season here is likely to select for rapid growth.

Growth rate of Curlew Sandpiper chicks in our field study was reduced during cold weather. Several mechanisms may underly this. Firstly, the time available for foraging for young chicks is reduced because they need increasing amounts of brooding when temperature decreases (Beintema & Visser 1989b; Visser & Ricklefs 1993a). Secondly, low temperatures and strong winds increase the chicks' energy expenditure for thermoregulation when not brooded by the parent. Thirdly, foraging success is likely to be reduced on cold days: we observed a strong decrease in surface activity of the arthropods on which the chicks feed. These mechanisms, singly or in combination, reduce the surplus of energy intake over expenditure that is necessary for growth.

Annual variation in breeding productivity

Although flyways between specific parts of the wintering and breeding ranges are not well separated in the Curlew Sandpiper, and birds wintering in South Africa may breed on Taimyr as well as further east (Underhill 1995), birds breeding in eastern Siberia are more likely to winter in southern Asia and Australia than in Africa. Thus, many of the Curlew Sandpipers wintering in South Africa probably originate from the large Taimyr population, and factors affecting their breeding success may be looked for in that area.

The weather station at the Pyasina delta is situated within the core of the Curlew Sandpiper's main breeding range on Taimyr (Lappo 1996). Although Pronchishchev Lake is situated c. 770 km to the NE on the opposite side of the peninsula, daily mean temperatures at the two sites were significantly correlated in late June-early August 1991 (r_{51} = 0.55, $P < 0.001$). A stronger correlation existed between mean temperature at the Pyasina Delta and at Pronchishchev Lake two days later (r_{51} = 0.74, $P < 0.001$), reflecting the generally eastward progression of weather systems across the peninsula. Therefore, we assumed that the Pyasina weather data are representative of general conditions across a major part of Taimyr.

Breeding productivity is composed of four sequential components: the proportion of females in the population producing a clutch, clutch size, clutch survival and chick survival. Clutch size variation is small in Curlew Sandpipers, as it is in arctic-breeding waders in general (Maclean 1972), and is therefore not expected to have a significant effect on breeding productivity. No data exist for Curlew Sandpipers on the size of any non-breeding segment of the adult population. The lack of a correlation between June weather and breeding productivity found in this study suggests that variation in this segment may not be substantial, or is independent of weather. Curlew Sandpipers show no breeding site fidelity (Underhill *et al.* 1993; Tomkovich & Soloviev 1994), and numbers in the southern part of the breeding range tend to increase in years of late snow melt (Haviland 1915; Hötker 1995; Lappo 1996), suggesting that females may avoid non-breeding years by settling in areas with better snow conditions.

Although there is variation in the viability of eggs, which may be weather-related (Tomkovich 1995), the main factor affecting hatching success is predation. This is indicated by the strong association between breeding productivity and lemming abundance (Summers & Underhill 1987; this study), and by the field observations at Pronchishchev Lake during the lemming peak of 1991, when all observed clutches hatched, and the following lemming low year, when only 1% of wader clutches, including Curlew Sandpipers', survived predation by Arctic Foxes and skuas (Underhill *et al.* 1993).

Chicks may become victims of predation too, but their survival is also affected by weather conditions and food availability. Cold weather increases the risk that chicks die of exposure, and

was shown in this study to reduce growth rate. This may lead to postponed fledging and prolonged exposure to predation. When adverse conditions prevail for more than a few days, they may result in starvation, as arctic wader chicks do not carry substantial fat reserves that can be invoked to overcome such periods (Norton 1973). Indeed, weather conditions in Taimyr during the main chick period explained a substantial part of the remaining variation in breeding productivity after inferred predation pressure had been accounted for. Given that the three defined levels of IPP and the proportion of juveniles in the South African winter catches are imperfect estimators of hatching success and breeding productivity respectively, the effects of weather on chick survival must be large and operate over an extensive geographical area to show up so clearly.

There have been few earlier attempts to relate breeding productivity of arctic-breeding waders to summer weather conditions, though Evans & Pienkowski (1984) proposed that 'the major factor affecting reproductive output would appear to be weather at high latitudes'. Boyd (1992) showed that changes in wintering numbers of Knots *Calidris canutus* in Britain were correlated with June temperatures in their Nearctic breeding range, but found no association between June temperatures, or other measures of summer weather, and the proportion or number of juveniles in the wintering population.

Effects of early breeding season weather on productivity have been demonstrated in several arctic-breeding geese (Boyd 1965, 1987; Kostin & Mooij 1995; Sheaffer & Malecki 1996; Skinner *et al.* 1998). Spring phenology affects the timing of laying and/or the female's energy budget during the prelaying period, which in combination determine clutch size, including the decision whether to breed at all (Uspenski 1965; Davies & Cooke 1983; Ganter & Cooke 1996). In contrast, Curlew Sandpiper productivity was correlated with conditions in the fledging period, but not with early spring weather. Wader chicks are less homeothermic than young waterfowl (Visser & Ricklefs 1993b), which renders the time that they can spend foraging instead of being brooded more sensitive to temperature. In addition, the food supply of insectivorous wader chicks is more sensitive to short-term variation in weather conditions than that of geese which take more plant material. Gardarsson & Einarsson (1997) did find productivity effects of weather and food availability during the fledging period in Wigeon *Anas penelope*, the chicks of which feed mainly on chironomids. Boyd (1996) reported correlations between the number of first-winter Long-tailed Ducks *Clangula hyemalis* shot in eastern North America and both summer and autumn temperatures in their breeding range. Since most goose studies have considered weather effects during the early part of the breeding season only, the suggestion that breeding productivity of arctic geese is more sensitive to conditions in the arctic spring, while waders are more affected by mid-summer weather, remains open for testing.

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SAMENVATTING

Sommige steltlopersoorten die broeden in arctisch Siberië, vertonen grote jaarlijkse fluctuaties in de aantallen jonge vogels tijdens de herfsttrek in NW-Europa en in de winter in (Zuid-)Afrika. Deze hangen gedeeltelijk samen met een driejaarlijkse cyclus in de aantallen lemmingen in de broedgebieden in Taimyr, die van invloed zijn op aantallen en prooikeuze (eieren of lemmingen) van predatoren. Om na te gaan of ook andere factoren, zoals weersomstandigheden, invloed hebben op het broedsucces, werd in 1991 in Noordoost-Taimyr een studie verricht naar de nog weinig bekende broedbiologie van Krombekstrandlopers *Calidris ferruginea*, met de nadruk op groei en gedrag in de kuikenperiode. Nesten lagen geconcentreerd in droge bultige delen van de toendra, maar wijfjes leidden hun jongen in de eerste week naar lager gelegen vochtigere plekken tot op ruim 2 km afstand. Hier werden vaak losse groepen gevormd van 2-6 broedsels waarvan de vrouwtjes samenwerkten bij het verjagen van predatoren, maar verder op hun eigen kuikens letten. 1991 was een lemming-piekjaar en de overleving van zowel nesten als kuikens was hoog; er werden c. 2 jongen per broedend vrouwtje vliegvlug. Het broedseizoen was sterk gesynchroniseerd en driekwart van de kuikens werd geboren tussen 10 en 15 juli. De groei verliep snel in vergelijking met andere steltlopersoorten, maar was wel vertraagd tijdens een koude periode. Hogere energieuitgaven en een kortere foerageertijd (doordat kuikens meer worden bebroed bij kou) kunnen hieraan hebben bijgedragen, maar ook werd vastgesteld dat de oppervlakte-aktiviteit van arthropoden, waarop de kuikens foerageren, sterk afnam bij lage temperaturen. Dat weersomstandigheden ook de overleving van de kuikens beïnvloeden, bleek uit een vergelijking van weersgegevens uit Taimyr met het aandeel eerstejaars vogels in ringvangsten in de winter in Zuid-Afrika over 18 jaren. Er werd een positief verband gevonden tussen temperatuur in de periode 11-20 juli, wanneer de meeste kleine jongen in de toendra aanwezig zijn, en de jongenproductie. Alleen in jaren met weinig lemmingen en een vermoedelijk hoge predatiedruk op legsels en kuikens was dit verband niet zichtbaar. Een combinatie van predatie en weersomstandigheden in de kuikenfase bepaalt dus in hoge mate het broedsucces van deze toendra-steltlopers. In tegenstelling tot wat bekend is van arctische ganzensoorten werd geen verband gevonden tussen broedsucces en weersomstandigheden aan het begin van het broedseizoen.

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